Stochastic Wilson-Cowan equations for networks of excitatory and inhibitory neurons II

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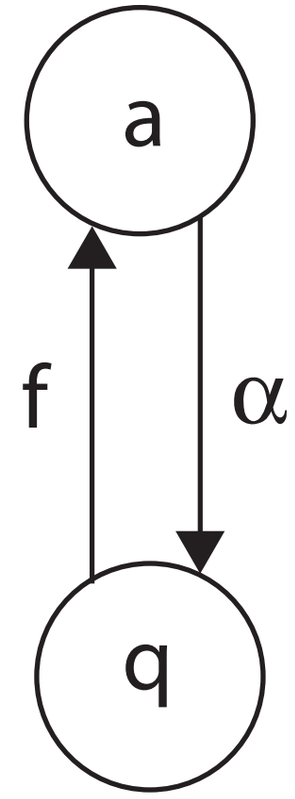
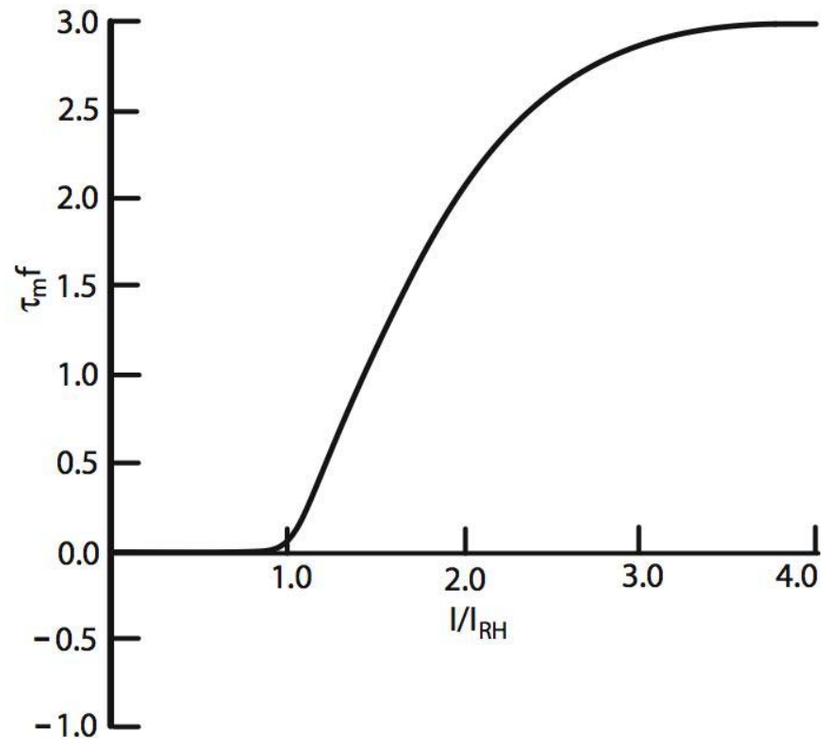
A simple Markov model of collective neural activation

Neurons are either quiescent or spiking at a rate f. q is the quiescent state and a the activated state, where q + a = 1, thus q and a are the proportions of cells in each state. Finally α is the rate at which activated cells become quiescent.



The function f is derived by looking at a population of integrate and fire neurons with fluctuating thresholds, and computing the fraction of neurons receiving at least threshold excitation I_{RH}.



$$f = \int_{-\infty}^{I_{\mathrm{RH}}} P(I)dI$$

$$f' = \sigma_{\mathrm{RH}}^2$$

A neural master equation

We can then write a *master equation* that involves the state transitions in a time Δt, which takes the form (for a homogeneous population of N excitatory neurons with all-to-all connections):

$$\frac{\partial P(n,t)}{\partial t} = \alpha(E^{-1}-1)nP(n,t) + (E^{+1}-1)(N-n)f[\frac{w_0}{N}n + h]P(n,t)$$

where $E^{+1}n = n+1, \quad E^{-1}n = n-1,$ n is the spiking rate, and P(n,t) is the probability that n spikes/unit time occur at time t, w_0 is the total net excitatory weight per neuron, h is an external stimulus.

From the master equation to the statistics of large-scale activity

Using techniques developed in quantum field theory and statistical mechanics we can transform the master equation into the following form:

$$\frac{\partial P(\varphi,t)}{\partial t} = \mathcal{H}(\varphi^*,\varphi)P(\varphi,t)$$

where

$$\mathcal{H}(\varphi^*,\varphi) = \int d^dx\,[\alpha\varphi^*\varphi - \varphi^*(\rho-\varphi_{\rm cl})f[w\star(\varphi^*\varphi+\varphi)+\alpha\varphi^*h]]$$

φ is a complex quantity associated with n(x,t)

φ^* is associated with *fluctuations* of n(x,t)

$\varphi_{\rm cl}$ is the mean field or classical value of φ.

From the master equation to a path integral

- We first replace the one-step operators E^{+1} and E^{-1} by the raising and lowering operators of the appropriate Lie algebra
- We then use the Schwinger decomposition to replace such operators by *creation* and *annihilation* operators using bosonic commutation rules
- Finally we replace these operators by *coherent states* built from them.
- Thus $E^{\pm 1} \longrightarrow \Lambda^{\pm 1} \longrightarrow \psi^\dagger \psi \longrightarrow \varphi^\star \varphi$ where $|\varphi\rangle = e^{(\varphi \psi^\dagger - \varphi^\star \psi)} |0\rangle$
- We then convert the resulting master equation to a path integral using standard methods

- The quantity $\mathcal{H}(\varphi^*, \varphi)$is the *quasi-Hamiltonian* of neural activity and the equation it satisfies is the analog of the diffusion equation in the theory of random walks, or the Schrödinger equation of quantum mechanics.

- To calculate statistics associated with such neural activity we form the quantity:

$$S(\varphi,\varphi^*) = \int_{-\infty}^{\infty} dt \left[\int d^d x \varphi^*(x,t) \frac{\partial \varphi(x,t)}{\partial t} + \mathcal{H}(\varphi^*(x,t), \varphi(x,t)) \right]$$

- This quantity is called the *neural action*. It can be used to generate equations for all statistical moments of the neural activity.

- In particular it generates the first moment or *mean-field* equation:

$$\frac{\partial \varphi_{\rm cl}(x,t)}{\partial t} = -\alpha \varphi_{\rm cl} + (\rho - \varphi_{\rm cl}) f[w \star \varphi_{\rm cl} + h_{\rm cl}]$$

Wilson & Cowan (1972, 1973).

- This equation has been the basis for many investigations of neural dynamics. But it does not include the effects of intrinsic neural *noise*, or of *correlations* in neural activity.

From the linearized part of the neural action it is easy to calculate the *Green's function* for the network dynamics from the path integral. In *Fourier* space it takes the simple form:

$$\langle \varphi(p,t)\varphi^*(p,t')\rangle = \exp\left[-(\alpha - f' \cdot \hat{w}(p))(t-t')\right]\Theta(t-t')$$

in case h=0.

But as $t \to \infty$ the Green's function or propagator approximates $G_0(p, t-t')$ the propagator for the diffusion limit of a random walk, or *Brownian motion*.

At long time scales neural activity is effectively analogous to a system of diffusing chemical reactions.

The power spectrum of spontaneous activity

Near a *critical point*, $\alpha = f' w_0$ the propagator for our field theory takes the form (in Fourier space):

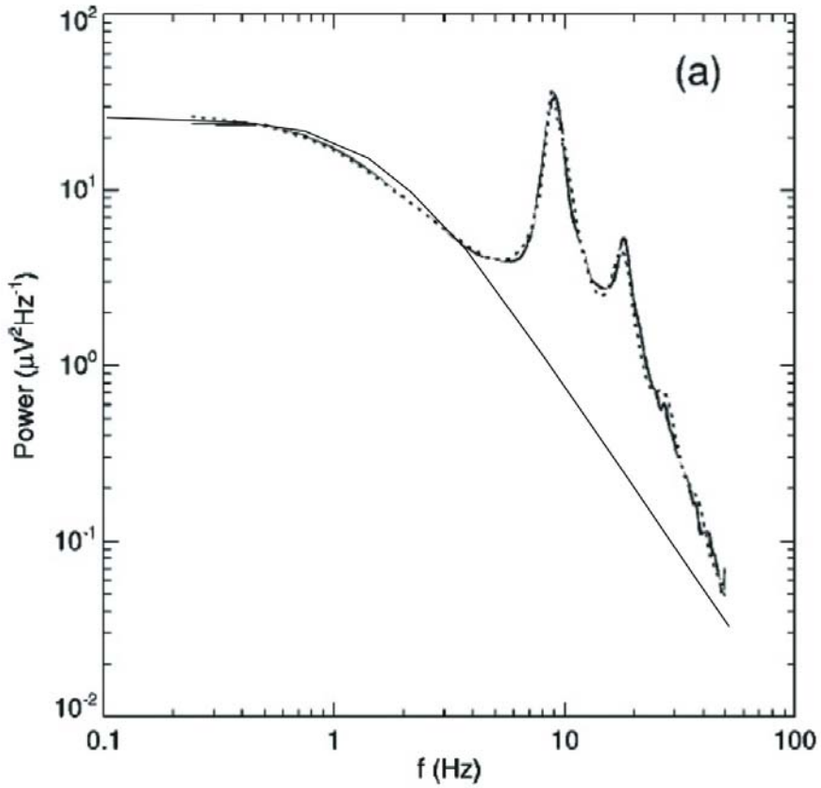
$$G(p, t - t') = \exp\left[-(\alpha - f' w_0 + \frac{1}{2} f' w_2 p^2)(t - t')\right] \Theta(t - t')$$

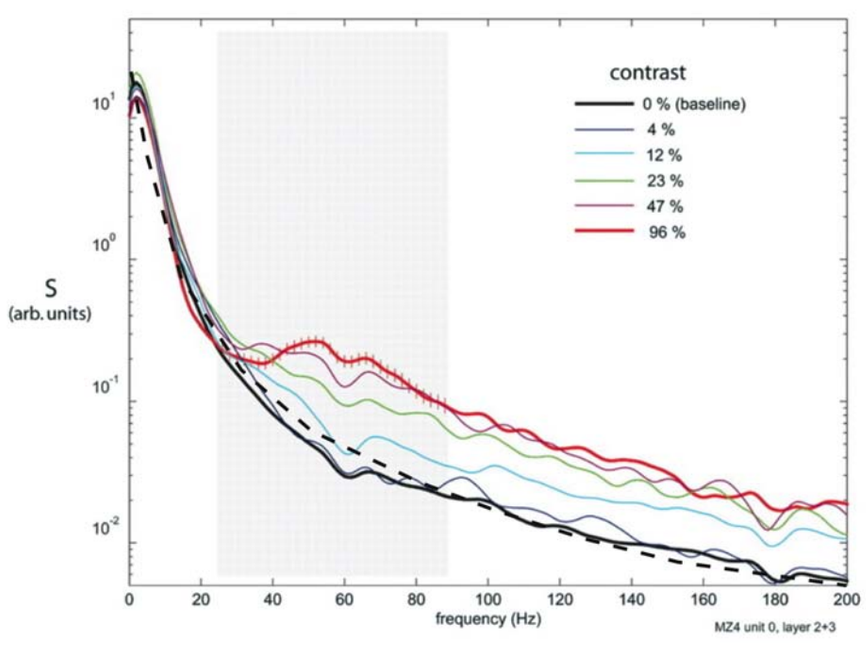
From this formula we can compute the power spectrum, which is proportional to

$$\left[(\alpha - f' w_0 + \frac{1}{2} f' w_2 p^2)^2 + \omega^2\right]^{-1}$$

Thus the *critical spectrum* for the spatially homogeneous mode, p = 0, is proportional to ω^{-2}

Power spectra of spontaneous activity derived from the field theory propagator





The nonlinear spike model

In more realistic neural models the firing rate function (or probability of spike generation) is nonlinear. We therefore approximate f(s) as

$$f(s) = f(s_0) + f'(s_0)(s - s_0) + \frac{f''(s_0)}{2!}(s - s_0)^2 + \cdots$$

The action is no longer quadratic and must be calculated by perturbation methods. *Renormalization group* methods can be used to solve this problem.

Renormalization

The problem is that in nonlinear systems the effects of multiple time and space scales need to be represented and addressed. When this is done the action is modified so that it correctly represents the dynamics on slow time scales and at long length scales. Such a *renormalized* neural Hamiltonian takes the form:

$$\mathcal{H}(\varphi,\varphi^*) = \int d^d x \left\{ \mu \varphi^* \varphi - D \varphi^* \nabla^2 \varphi + g \cdot [\varphi^2 \varphi^* - \varphi^{*2} \varphi] \right\}.$$

where $$D = f' \int d^d x x^2 w(x) = f' w_2$$

and μ and g are renormalized constants.

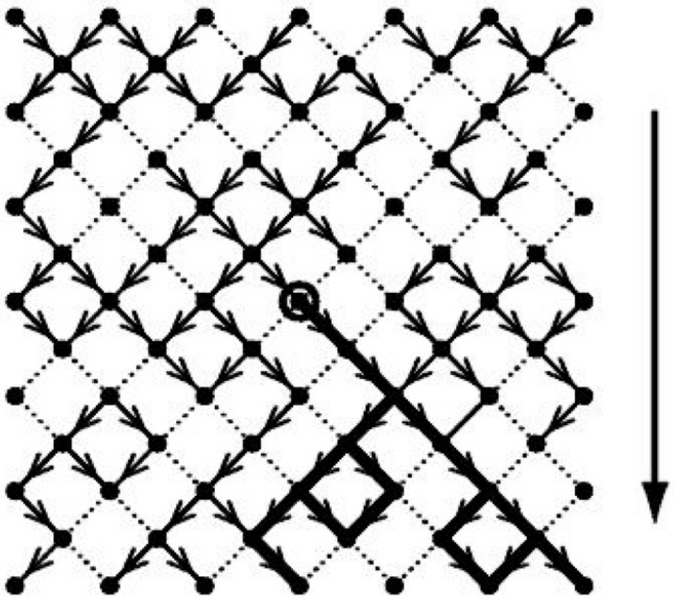
Reggeon field theory

But the renormalized action is exactly that of *Reggeon field theory*, introduced by Gribov to model some aspects of high energy particle physics. It was shown about a decade ago by Cardy and Sugar that it corresponds to a system with both branching and aggregation, called *directed percolation*. If the dynamics is *critical*, as in the neural case when $\alpha = f' w_0$, Cardy and Sugar showed that such a system has a universal non-equilibrium *phase transition*, i.e., a directed percolation (DP) phase transition.

DP neural phase transitions

Thus the *dynamically balanced* equilibrium states of neural nets should exhibit a DP phase transition when such states are destabilized, either spontaneously or by the action of applied currents. In such a case *large fluctuations* and *long-range spatio-temporal correlations* should appear. Well away from such states, mean field behavior without correlations should occur.

Directed Percolation



$p<p_c$ $p=p_c$ $p>p_c$

A Ginzburg condition for the emergence of directed percolation

We can derive a condition for the emergence of the DP phase transition. It takes the form:

$$(\frac{w_2}{w_0})^2 \gg \zeta \frac{|f''|w_0 A}{f'} L_d^{4-d}$$

where $L_d = \sqrt{\frac{f'w_2}{2(\alpha - f'w_0)}}$ is the "diffusion" length for the spread of the activity and A is a renormalization constant. If this condition holds then critical branching without aggregation occurs.

Critical exponents for DP

Exponents	$d=1$	$d=2$	$d=3$	$d=4$
β	0.276	0.583	0.805	1
$\nu_\perp$	1.097	0.733	0.581	1/2
$\nu_\parallel$	1.734	1.295	1.105	1
τ	1.108	1.268	1.395	3/2

What is the effective dimensionality *d* of the neocortex?

$$d \approx log_2 k$$

where *k* is the number of contacts per neuron. We take k to be between 4000 and 10000, whence $d \approx 12$

Critical exponents: neural case

- Because of the high degree of neural connectivity it is likely that *the neural phase transition is mean field DP.* Thus the renormalized propagators reduce to the following:

- (a) subcritical:

$$G(x-x',t-t') \propto (t-t')^{-2}\exp[-\frac{(x-x')^2}{4(t-t')}-\mu(t-t')]$$

- (b) critical:

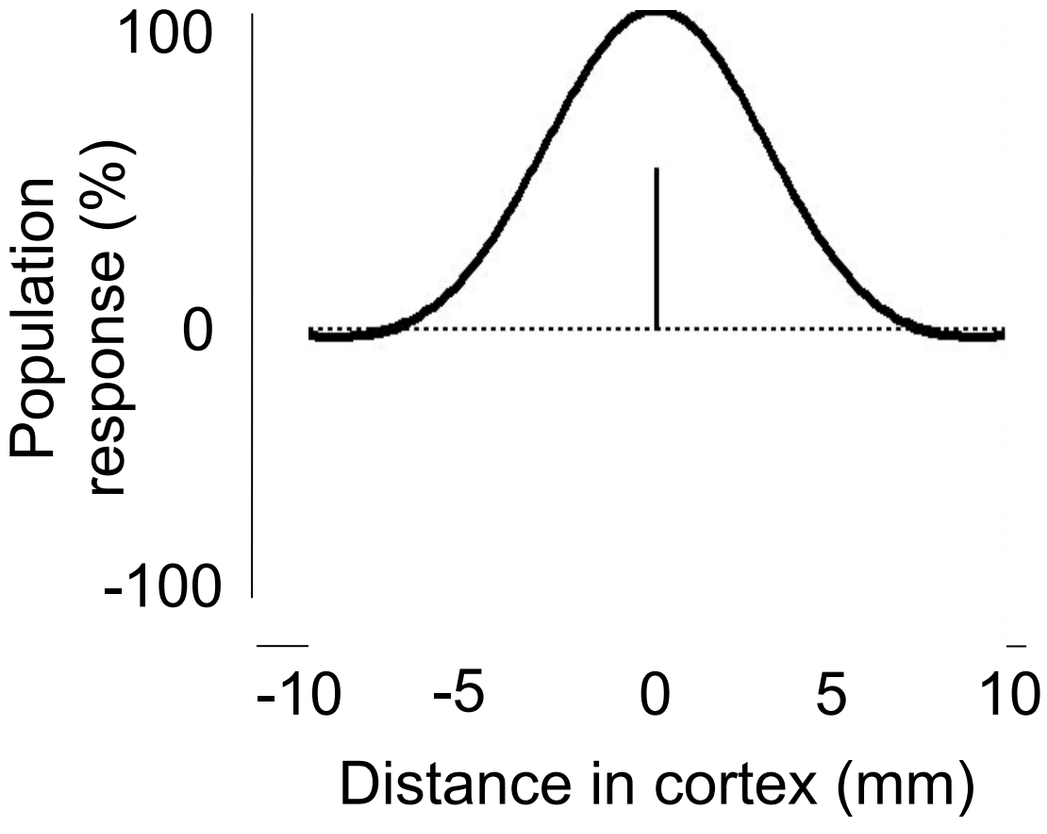
$$G(x-x',t-t') \propto (t-t')^{-2}\exp[-\frac{(x-x')^2}{4(t-t')}]$$

- (c) supercritical:

$$G(x-x',t-t') \propto \mu^2\Theta[\sqrt{|\mu|}(t-t')-|x-x'|]$$

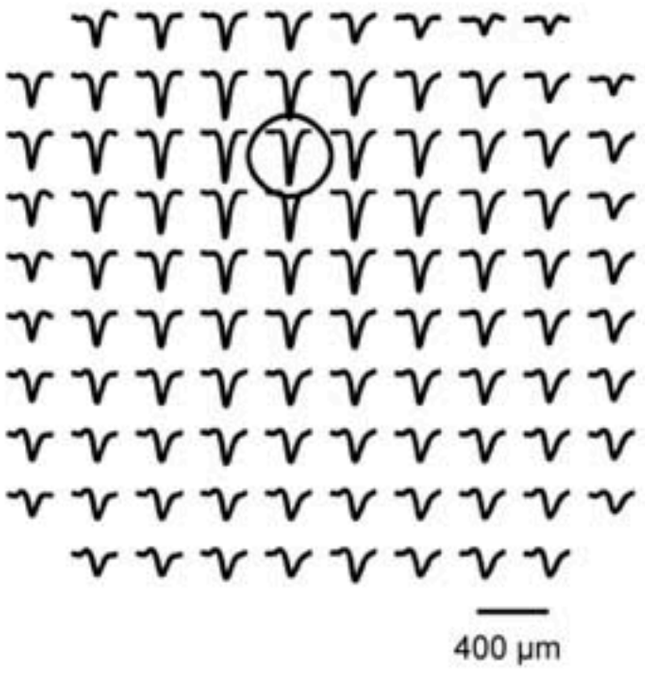
Cortical

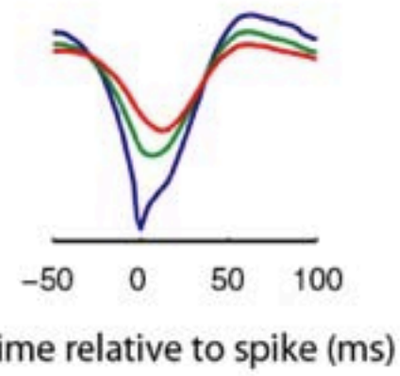
The dampened traveling wave
(Carandini '09)



Single spikes elicit waves in the local field potential

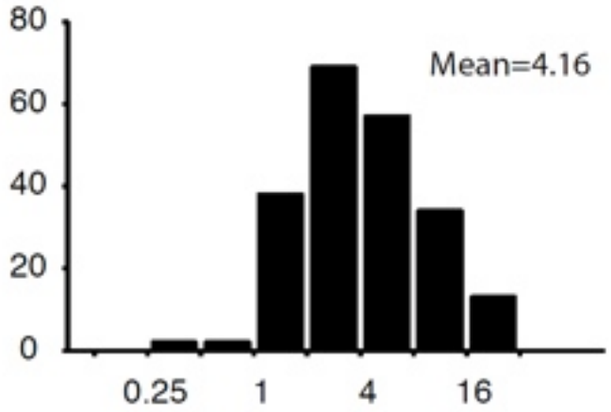
The slightly subcritical state



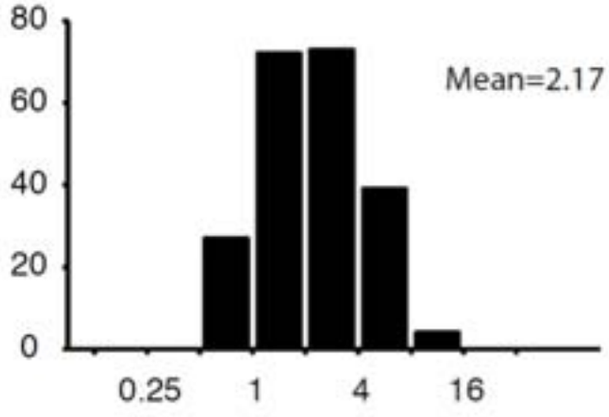


Nauhaus, Busse, Carandini, & Ringach, *Nature Neurosci*, 2009

Contrast decreases wave spread and magnitude



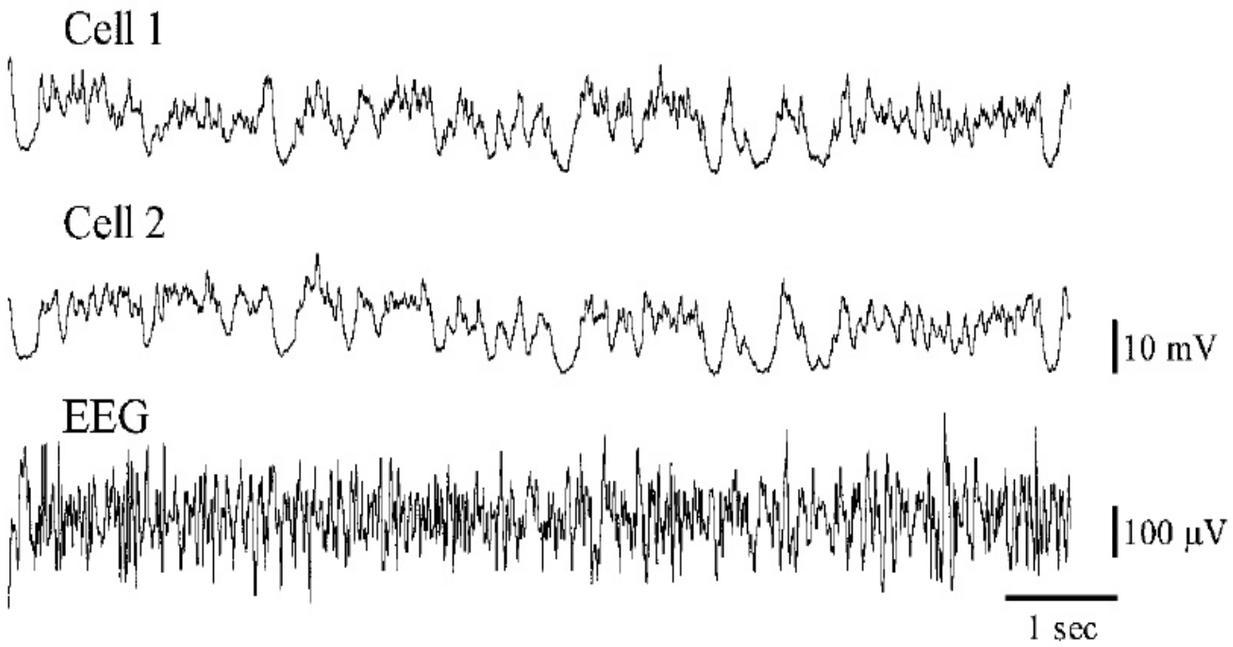
Decrease in space constant

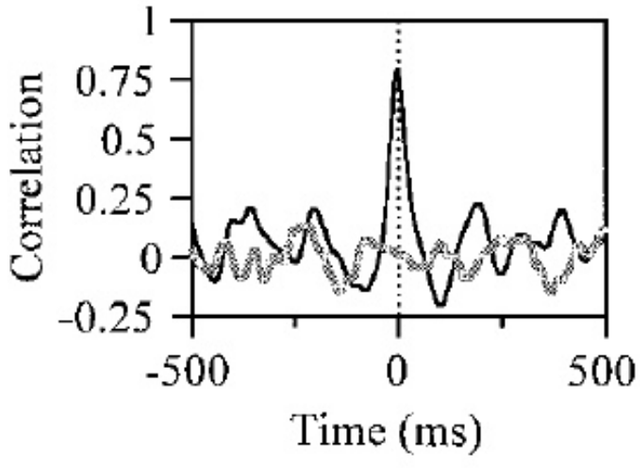


Decrease in magnitude

Nauhaus, Busse, Carandini, & Ringach, *Nature Neurosci,*

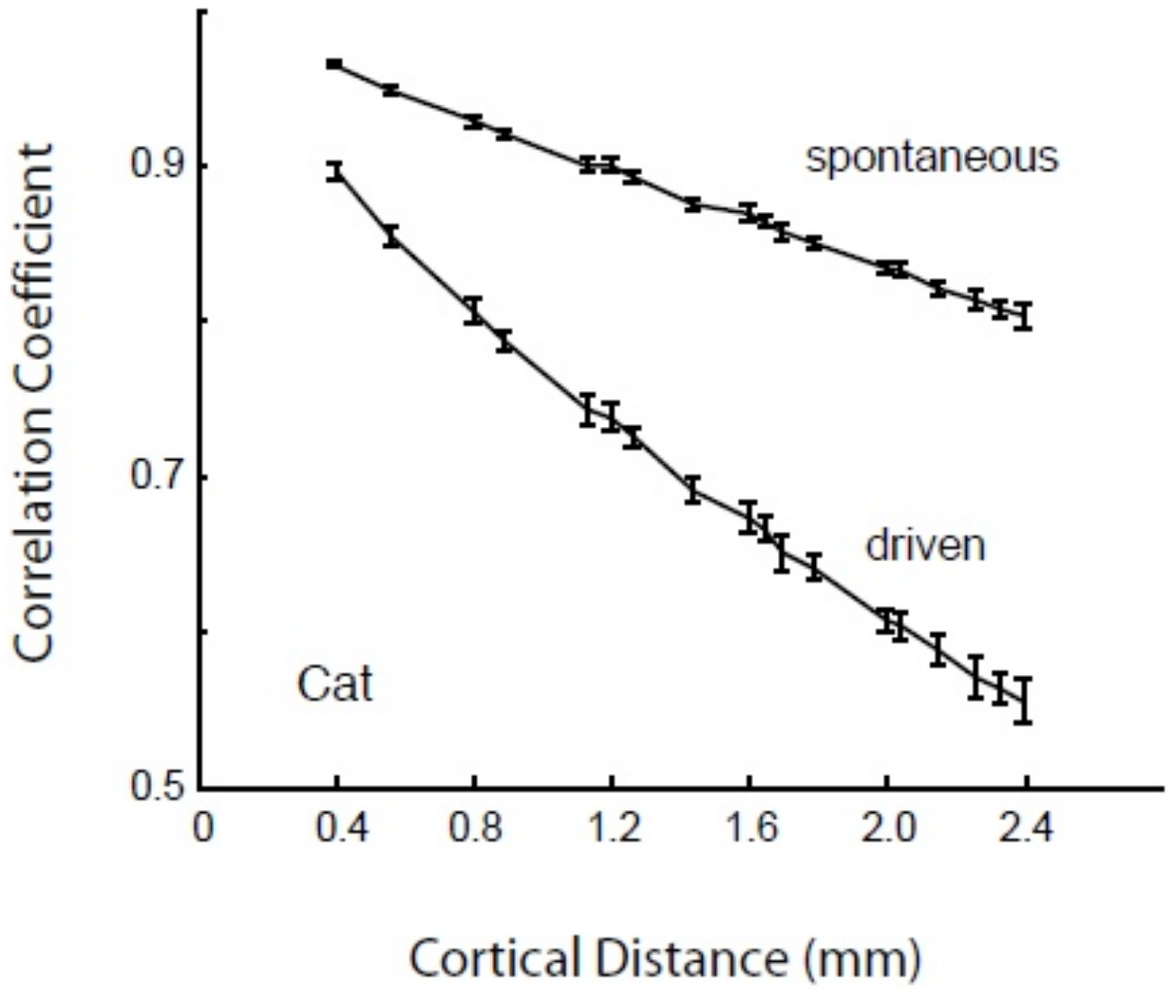
Strong correlation among pairs of cells





Lampl, Reichova & Ferster *Neuron*

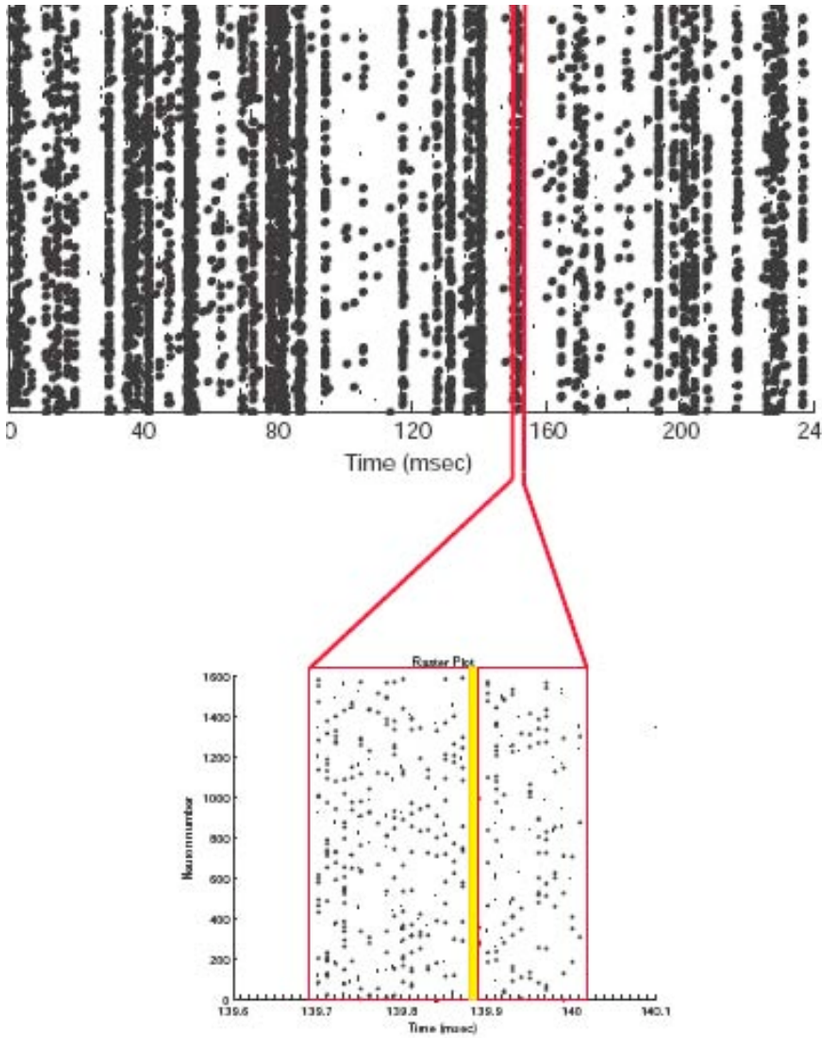
Effect of contrast on correlation between LFPs



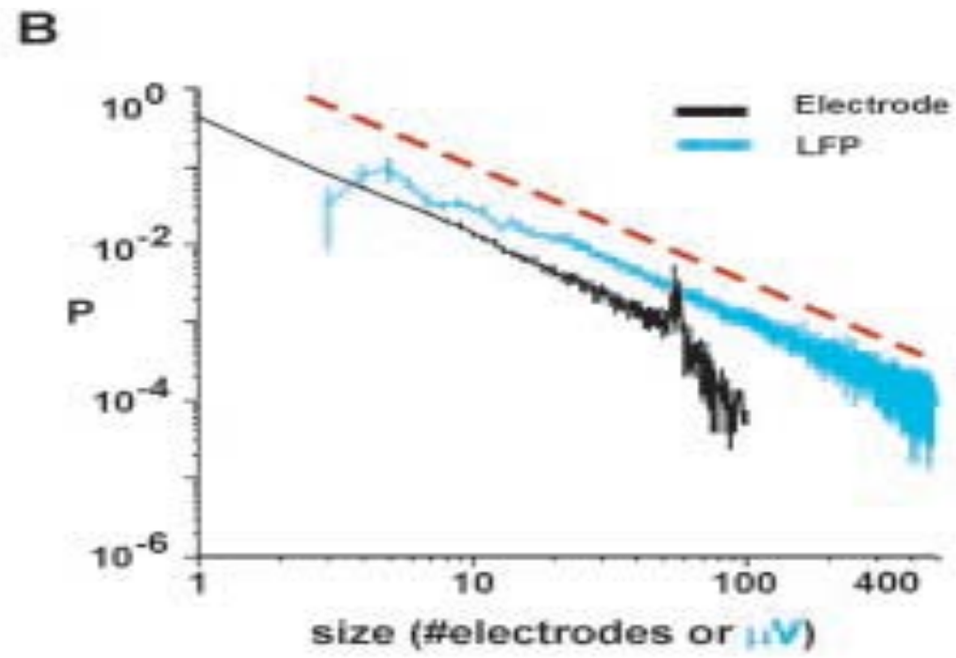
Nauhaus, Busse, Carandini, & Ringach, *Nature Neurosci,*

Spontaneous activity

Noise driven neural activity has scale-free properties (Beggs-Plenz)



Avalanche size distribution



Critical branching

In addition, as long as the weighting function w(x,x') is spatially homogeneous, i.e. is of the form w(x-x') the action given above exactly represents a *branching process* with branching rate

$$w_0 = \int d^d x w(x)$$

and decay rate α . Thus when $\alpha = f' w_0$ *critical branching* should be observed.

A field theory calculation

The avalanche size distribution P(s) can be expressed as:

$$P(s) = s^{\alpha}, \quad \alpha = -\left[1 + \frac{\beta}{\nu(4+z) - \beta}\right]$$

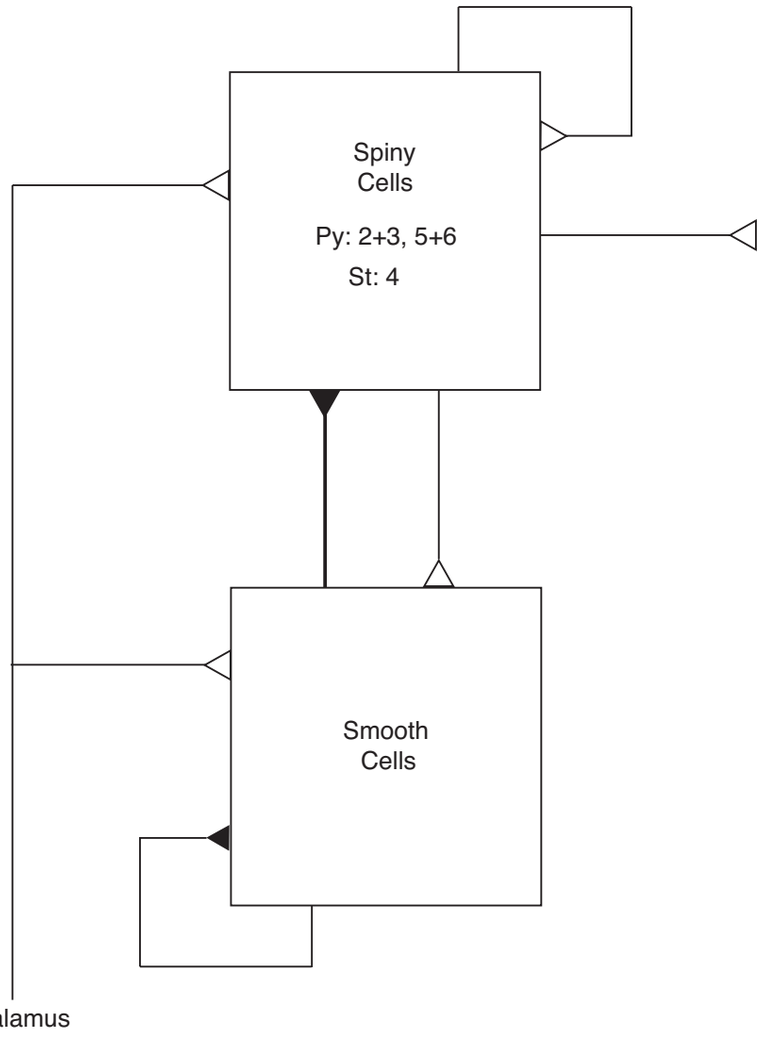
The mean-field exponents for DP are:

$$\beta = 1, \quad \nu = \frac{1}{2}, \quad z = 2$$

whence: $\alpha = -\frac{3}{2}$.

A field theory of canonical microcircuits comprising both excitatory and inhibitory neural populations

- In 1991 Douglas & Martin introduced the canonical microcircuit as a model of the local modular neocortical circuit.



Reducing the E-I renormalized action to the RFT action

The renormalized E-I action can be written in the form:

$$\int\int d^d x dt \left[\tilde{s}_1(\partial_t + \mu_1 - D_1\nabla^2)s_1 - g_{12}s_2 - g_1\tilde{s}_1(s_1 - \tilde{s}_1)s_1\right.$$
$$+\tilde{s}_2(\partial_t + \mu_2 - D_2\nabla^2)s_2 + g_{21}s_1 - g_2\tilde{s}_2(s_2 - \tilde{s}_2)s_2$$
$$\left.+1/2(\tilde{s}_1 h_{12} + \tilde{s}_2 h_{21})s_1 s_2 + \cdots\right]$$

The linear part of this action is:

$$\int\int d^d x dt \left[\tilde{s}_1(\partial_t + \mu_1 - D_1\nabla^2)s_1 - g_{12}s_2 + \tilde{s}_2(\partial_t + \mu_2 - D_2\nabla^2)s_2 - g_{21}s_1\right]$$

This gives rise to the eigenvalue problem

$$\begin{pmatrix} \mu_1 + D_1 p^2 & -g_{12} \\ g_{21} & \mu_2 + D_2 p^2 \end{pmatrix} \begin{pmatrix} \hat{s}_1 \\ \hat{s}_2 \end{pmatrix} = \begin{pmatrix} \lambda_1 & \cdot \\ \cdot & \lambda_2 \end{pmatrix} \begin{pmatrix} \hat{s}_1 \\ \hat{s}_2 \end{pmatrix}$$

with solution

$$\lambda_\pm = \frac{1}{2}\left(\mathrm{Tr}A \pm \sqrt{\mathrm{Tr}^2 A - 4\mathrm{Det}A}\right)$$

where A is the matrix

$$\begin{pmatrix} \mu_1 + D_1 p^2 & -g_{12} \\ g_{21} & \mu_2 + D_2 p^2 \end{pmatrix}$$

Evidently the eigenvalues are *real* iff $\mathrm{Det}A \leq \frac{1}{4}\mathrm{Tr}^2 A$ and complex iff $\mathrm{Det}A > \frac{1}{4}\mathrm{Tr}^2 A$. These conditions together with $\mathrm{Tr}A < 0$ define a stable *node* and a stable *focus*. However if $\mathrm{Tr}A = 0$ a stable *limit cycle* emerges.

Analogy with stochastic Lotka-Volterra equations on a lattice

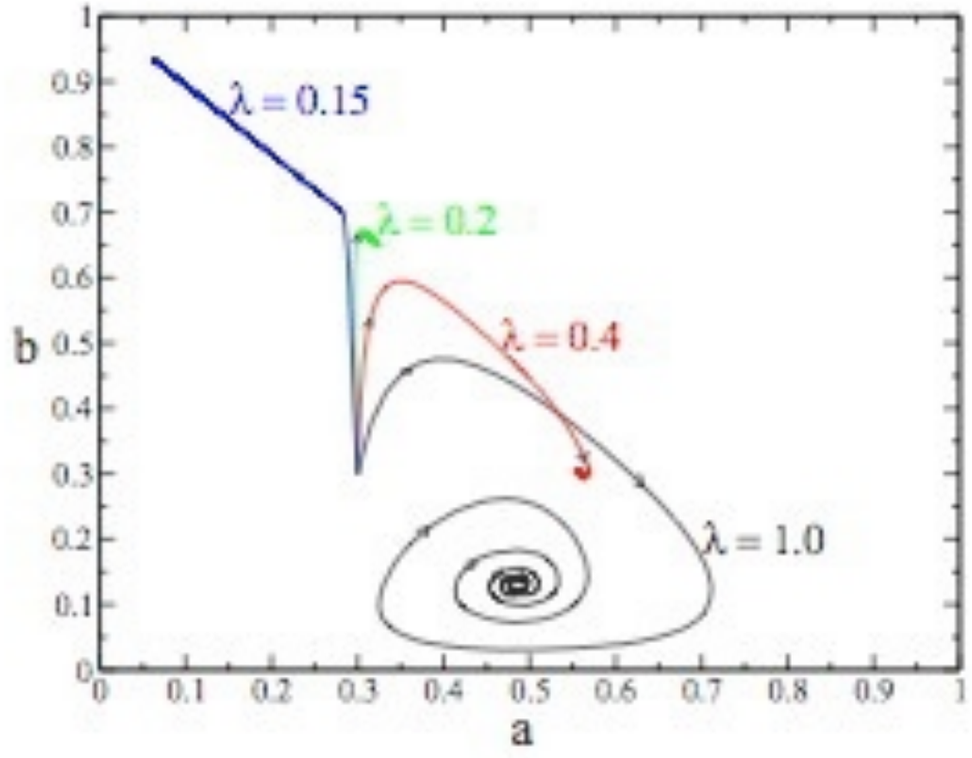
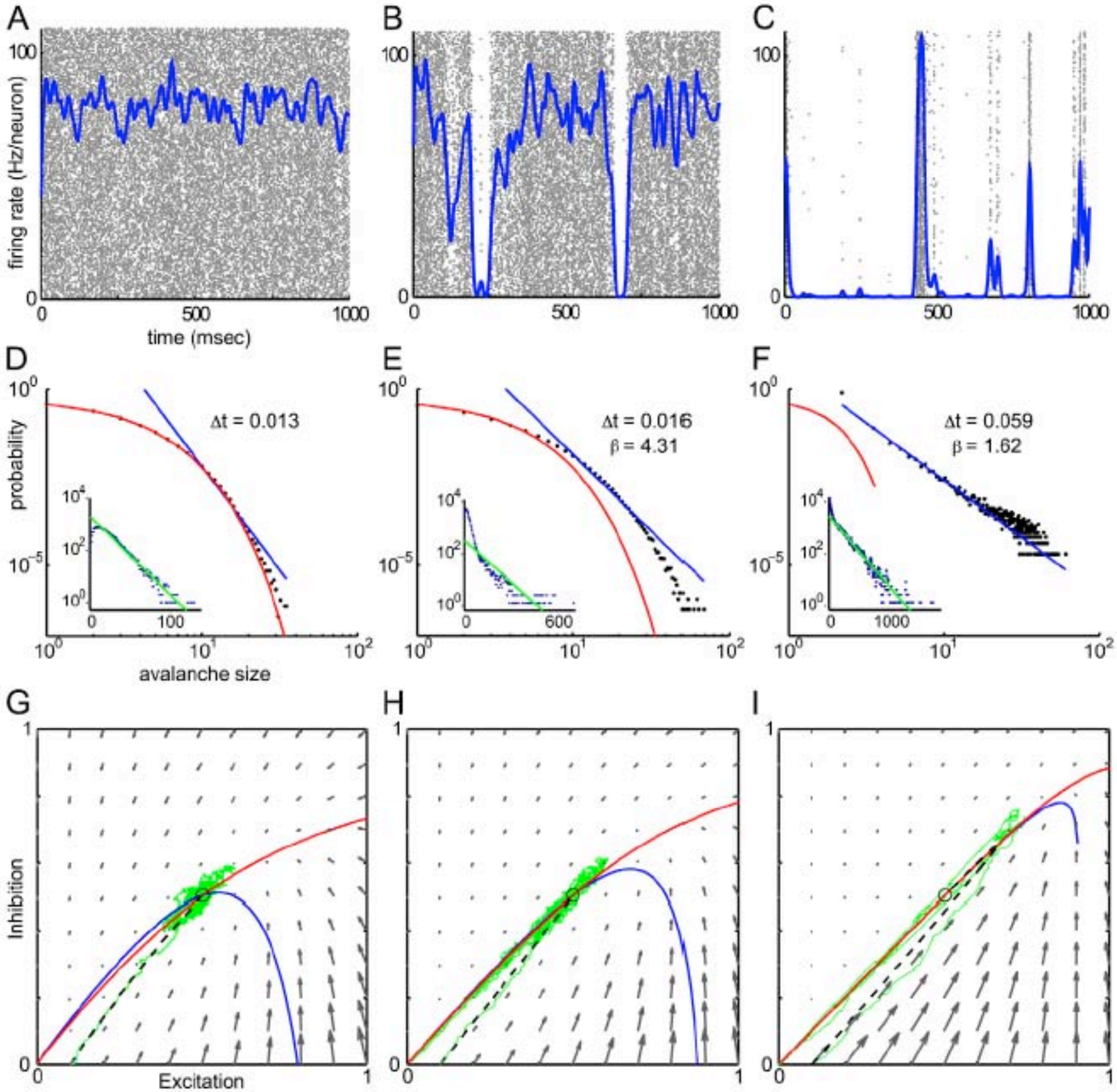
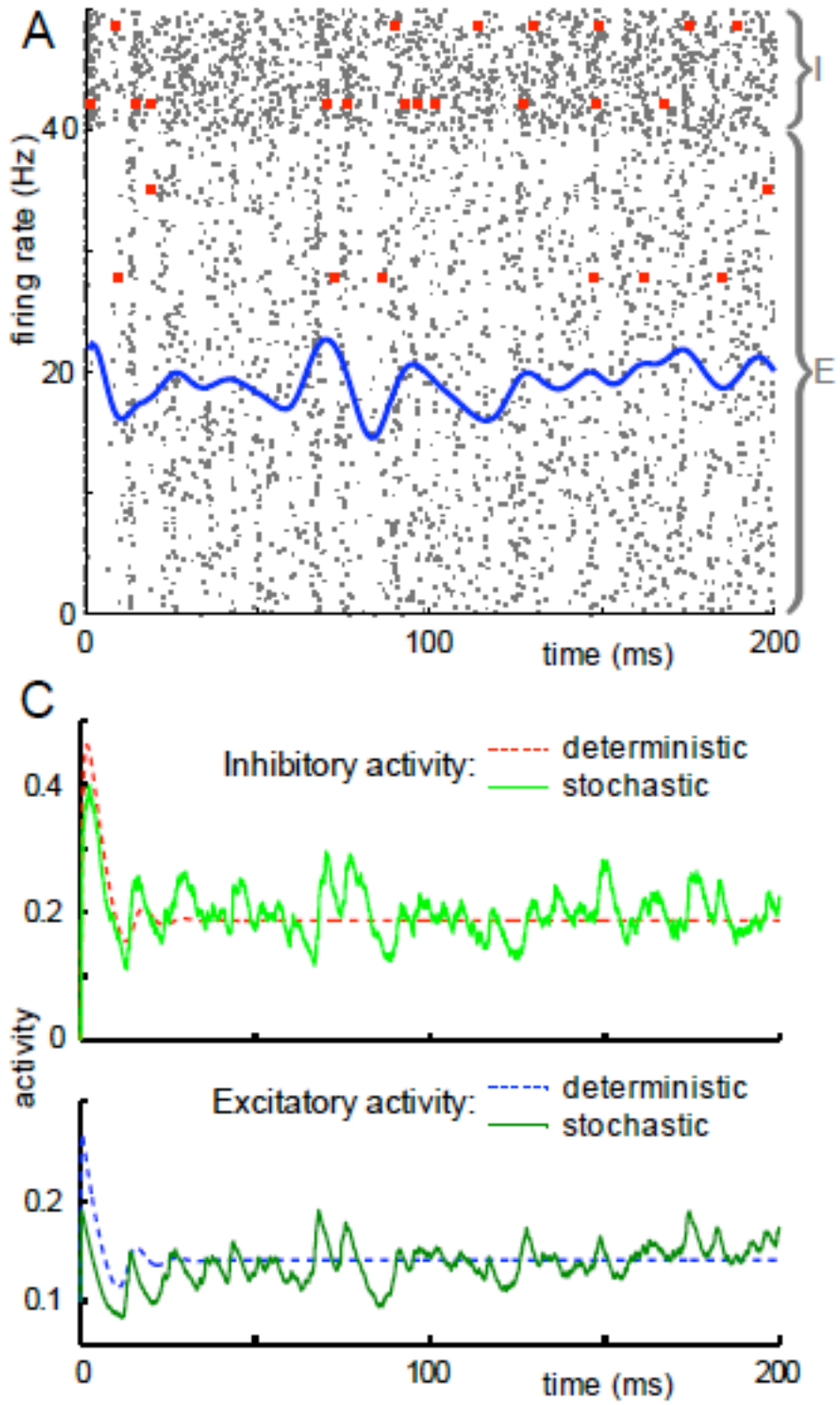


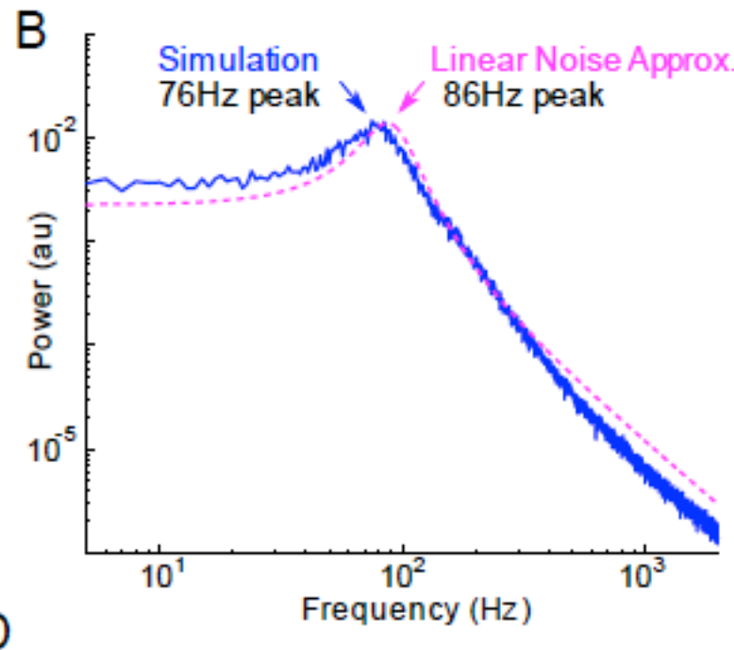
Fig. 1. (Color online.) Typical trajectories in the predator/prey coexistence phase depicting the phase portrait for the NN model on a (512 × 512) lattice. All runs start from random initial configuration with $a(0) = b(0) = 0.3$ and fixed rates $D = 0$, $\sigma = 4.0$, $\mu = 0.1$, and $\lambda = 0.15, 0.20, 0.40, 1.0$, respectively. For high values of λ we observe the typical spirals (the fixed point is a focus) in phase space, while for small values of λ (typically $\lambda < 0.4$) the fixed point is a node.

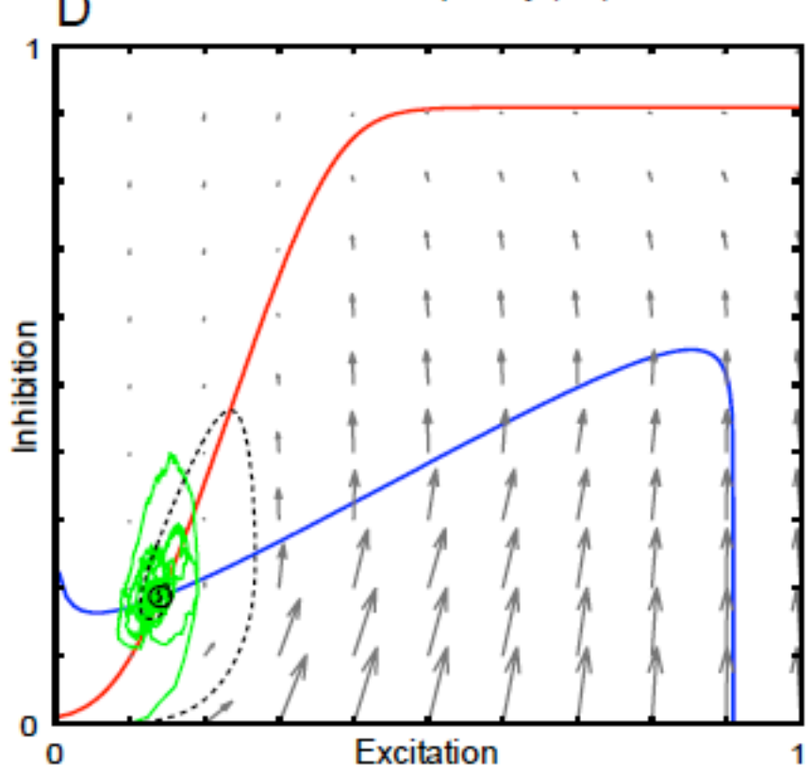
Avalanche formation



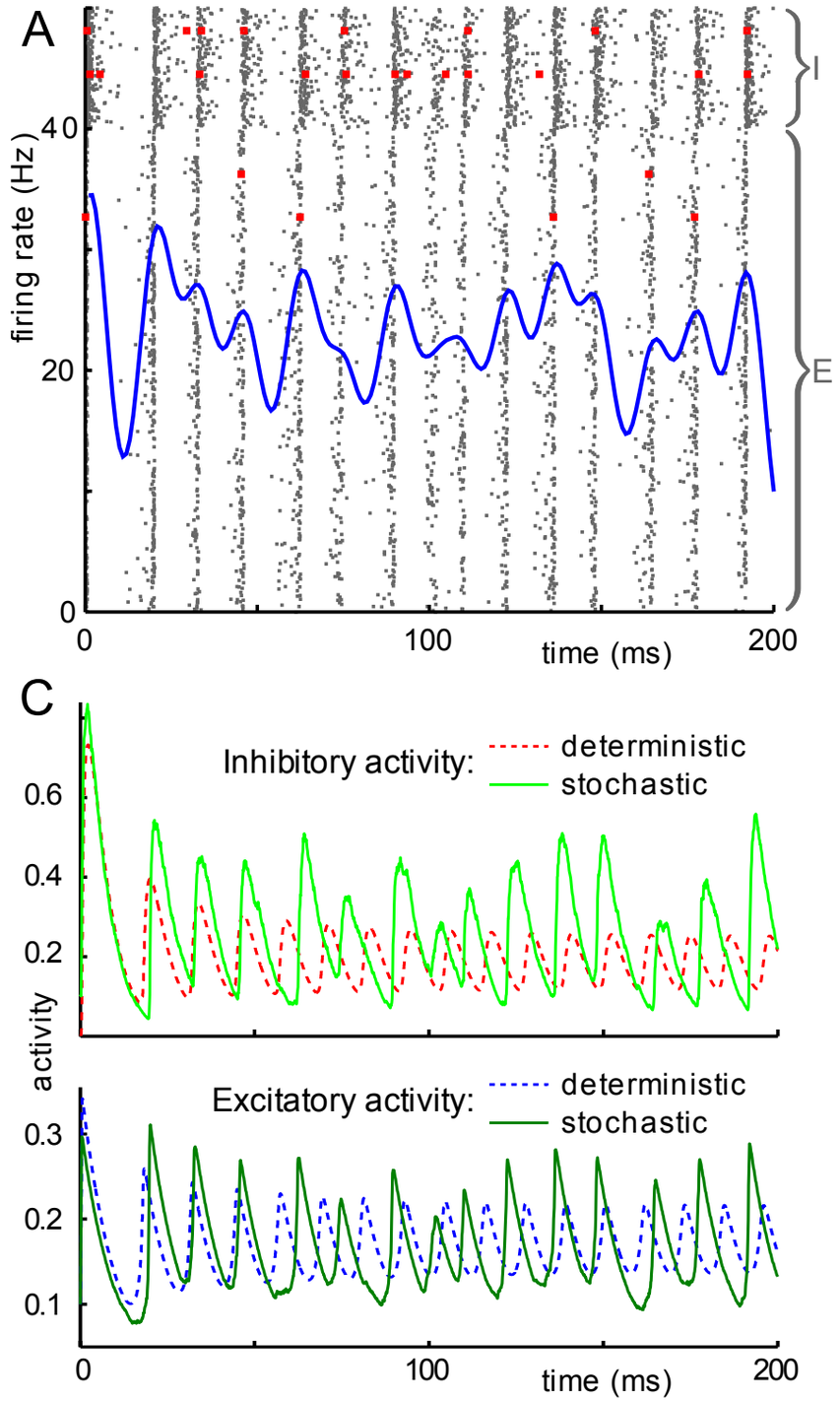
Population oscillation formation

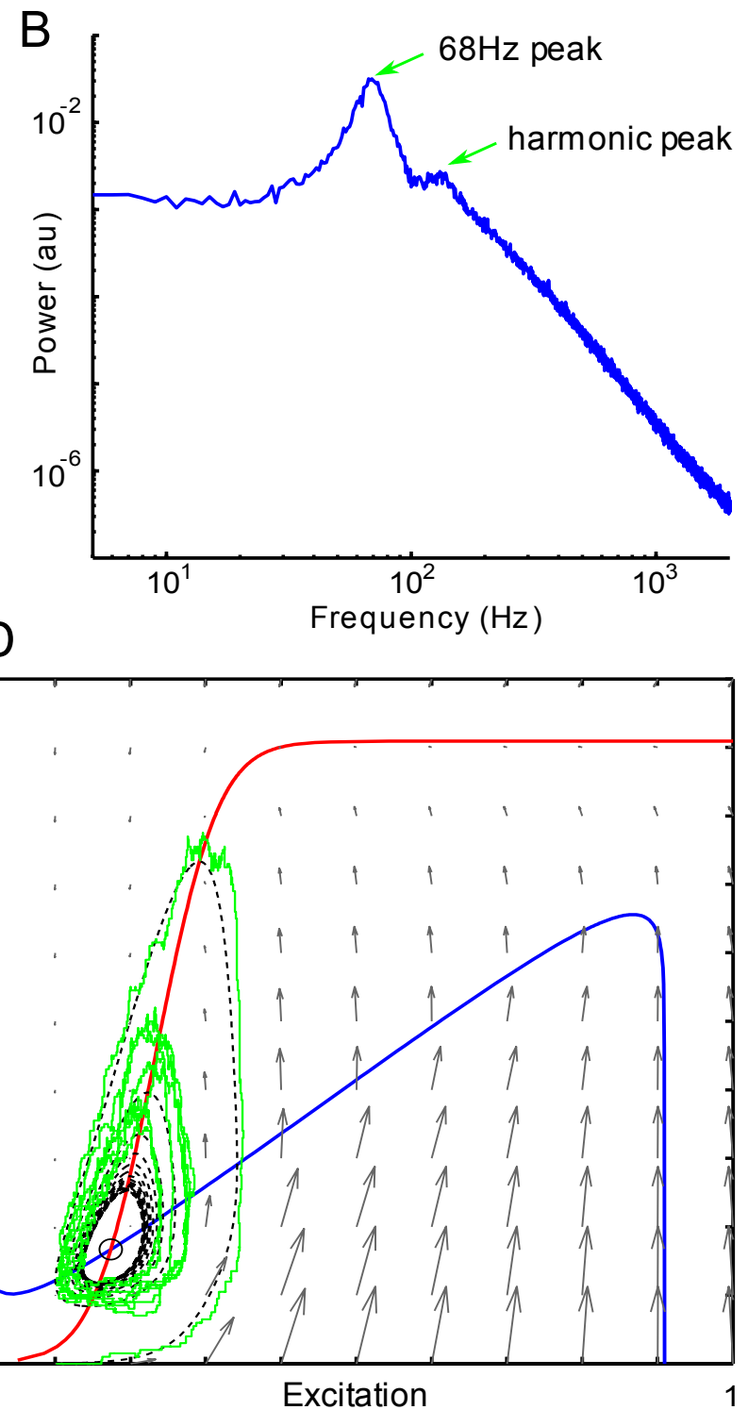






Limit cycle formation





We now introduce two mechanisms for reducing the renormalized E-I action to the RFT action:

(a) *The neural analog of predator extinction in stochastic Lotka-Volterra dynamics*
(b) *Balanced excitation and inhibition*

In case (a) examination of the eigenvalue equation indicates that the coupling coefficents $g_{\alpha\beta}$ determine the transition from node to focus to limit cycle. As $g_{\alpha\beta} \to 0$, s_1 and s_2 become uncoupled so that $s_2 \to 0$ and $s_1 \to s_1^\star$ and we end up with the RFT action

$$\int\int d^d x dt \left[\tilde{s}_2(\partial_t + \mu_2 - D_2\nabla^2)s_2 + g_2\tilde{s}_2(s_2 - \tilde{s}_2)s_2\right]$$

(b) *Balanced excitation and inhibition*

We next look at a special (symmetric) case of the renormalized E-I action:

$$\mu_1 = \mu_2 = \mu; D_1 = D_2 = D;$$

$$g_1 = g_2 = g; g_{12} = g_{21}; h_{12} + h_{21} = 2g$$

and let

$$s_1 + s_2 = s, s_1 - s_2 = c; \tilde{s}_1 + \tilde{s}_2 = 2\tilde{s}, \tilde{s}_1 - \tilde{s}_2 = 2\tilde{c}$$

This is essentially the same transformation used in Benayoun et al (2010). The E-I balance condition $s_1 = s_2$ then implies $c = 0, \tilde{c} = 0$, and once again the E-I action reduces to the RFT action. But note that in such a case $s = s_1 + s_2 = 2s_1 = 2s_2$.

Critical behavior of the E-I system

- The condition E-I << E+I underlies the generation of avalanches about a stable node.
- This condition generates the DP phase transition even in coupled E-I populations
- Avalanches can occur close to but below criticality
- Population oscillations and limit cycles can also occur at stable attractors close to but below criticality

Criticality and the E/I balance

- If $w_E < w_I$; *subcritical*, inhibition dominated
- If $w_E = w_I$; *slightly subcritical*, balanced
- If $w_E = w_I + \alpha/f'$; *critical*, lightly excited
- If $w_E > w_I + \alpha/f'$; *supercritical*, excitation dominated

Conclusions

- It is possible to construct a neural field theory which predicts the existence of a neural non-equilibrium phase transition in the same universality class as *directed percolation*. This has a variety of experimental consequences.

This work was carried out with four former U of C graduate students, Toru Ohira (Physics, 1993), Michael Buice (Physics, 2005), Marc Benayoun (Pediatric Neurology, 2010) and Edward Wallace (Mathematics, 2010), and since 2009 in collaboration with Wim VanDrongelen (U of C), and more recently with Nigel Goldenfeld (University of Illinois) and Tom Butler (MIT).